

1           **Artificial structures alter kelp functioning across an urbanised estuary**

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15       Running title: Infrastructure and kelp functioning

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17 **Abstract**

18

19 Assessments of human impacts on natural habitats often focus on the abundance of  
20 component species, yet sub-lethal effects of stressors on functional attributes may be  
21 equally important to consider. Here we evaluated how the addition of artificial  
22 structures, an integral part of urbanisation in the marine environment, affects key  
23 functional properties of the habitat-forming kelp *Ecklonia radiata*. Given that  
24 stressors rarely occur in isolation, we assessed the effects of infrastructure across an  
25 urbanised estuary. Estuaries are ideal for studying how multiple anthropogenic and  
26 natural stressors influence potential impacts of infrastructure on habitat-forming  
27 species because these habitats usually face a wide range and levels of stressors. Here,  
28 we compared the abundance, growth, erosion and photosynthetic activity of kelps in  
29 artificial and natural habitats across one of the largest urbanised estuaries in the world  
30 - Sydney Harbour. We predicted that effects of artificial structures on functional  
31 attributes of kelps would be stronger in the inner area of the Harbour, characterised by  
32 higher levels of human impacts and low flushing. Contrary to our predictions, we  
33 found that effects of infrastructure were consistent across the estuary, regardless of  
34 the ecological footprint caused by human activities or natural environmental  
35 gradients. When differences were observed between areas of the estuary, they mostly  
36 occurred independently of impacts of substrate type. Importantly, we found lower  
37 erosion rates of kelps on pilings than on reefs, likely resulting in lower production of  
38 detritus in places where artificial structures have replaced or fragmented natural  
39 habitats. Such impacts have important implications for the connectivity among coastal  
40 habitats and secondary productivity in adjacent and remote habitats, which are highly  
41 dependent on the exportation of kelp detritus. Our study is the first to assess potential  
42 functional consequences of urbanisation through physiological effects on habitat-

43 formers, a severely overlooked mechanism of environmental impact on ecosystem  
44 functioning.  
45  
46 Key-words: *Ecklonia radiata*, *Sargassum* spp., growth-rates, urbanisation, habitat-  
47 formers, ecosystem functioning

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48 **Introduction**

49 Foundation or habitat-forming species such as trees, seaweeds and corals  
50 underpin great diversity and important functions of natural systems (Dayton 1972,  
51 Bruno and Bertness 2001, Ellison et al. 2005). Because of their structural and  
52 functional attributes, these habitat-formers create and define entire communities and  
53 ecosystems and can modulate several ecological and biogeochemical processes  
54 (Ellison et al. 2005) - many of which are directly linked to the provision of services  
55 and goods (Christensen et al. 1996, DeFries et al. 2004). Anthropogenic impacts on  
56 ecosystem functioning, and consequently on ecosystem services, can therefore occur  
57 through impacts on the abundance and diversity of habitat-formers, or through effects  
58 on their physiology, metabolism and/or behaviour (Díaz et al. 2007). Nevertheless,  
59 assessments of human impacts often focus on the abundance of these key species (e.g.  
60 Harding et al. 2001, Phillips and Blackshaw 2011), overlooking potential  
61 physiological effects of stressors on their functional attributes, which may be equally  
62 important to consider.

63 Habitat modification is of major concern worldwide and one of the main  
64 drivers of loss of biodiversity (Foley et al. 2005). Amongst the most widespread  
65 forms of habitat modification in recent decades is the addition of built infrastructure  
66 such as buildings and roads on land (Trombulak and Frissell 2000) and seawalls and  
67 pilings in the marine environment (Bulleri and Chapman 2010). While the effects of  
68 habitat modification on the abundance and diversity of habitat-formers are relatively  
69 well-studied (Steneck et al. 2002, Ellison et al. 2005, Foley et al. 2005, Grimm et al.  
70 2008), possible sub-lethal impacts and their implications for the overall functioning of  
71 systems are much less understood. Understanding the effects of artificial structures on

72 functional attributes of habitat-formers is essential to evaluate the full potential  
73 consequences of habitat modification on the functioning of systems.

74         The addition of built infrastructure is transforming landscapes across the  
75 globe, and is associated with decreased biodiversity (Chapman 2003, Mayer-Pinto et  
76 al. 2018), homogenization of biota (McKinney 2006, Bulleri and Chapman 2010) and  
77 increased abundances of invasive species (McKinney and Lockwood 1999, Dafforn et  
78 al. 2012a, Airoidi et al. 2015). These artificial structures can affect the ecology of  
79 habitat-formers through a variety of mechanisms. Roads, for instance, can affect  
80 plants directly through land clearings and/or indirectly through changes in soil's  
81 chemical and physical composition and increased contamination (Trombulak and  
82 Frissell 2000), potentially reducing their growth and seed germination (Peralta et al.  
83 2001) and increasing abundances of weeds (Hansen and Clevenger 2005, Meunier and  
84 Lavoie 2012). Similarly, in estuaries, seawalls can affect seaweeds by directly altering  
85 or replacing natural settlement surfaces (Goodsell et al. 2007, Goodsell 2009) and/or  
86 by modifying their surrounding environment through changes in water flow and  
87 nutrient availability (e.g. Bishop et al. 2017) and ecological interactions e.g. reduction  
88 in grazers (Chapman 2003, Klein et al. 2011). Artificial structures may also facilitate  
89 invasion of macro-algae species on natural habitats through increases in propagule  
90 pressure (Epstein and Smale 2017). Furthermore, stressors rarely occur in isolation  
91 and pressures from built infrastructure are often compounded by associated  
92 anthropogenic activities leading to e.g. increased contamination, resulting in degraded  
93 air, soil, sediment and water quality (McGee et al. 1995, Trombulak and Frissell 2000,  
94 Van Bohemen and Van De Laak 2003, Dafforn et al. 2015). These urban pressures  
95 can significantly influence the functional attributes of habitat-forming species, with  
96 potential interactive effects (Crain et al. 2008).

97 Underwater forests comprised of habitat-forming kelps, like many of their  
98 terrestrial counterparts, are in significant decline around the world as a result of  
99 coastal urbanisation (Tibbetts 2002, Coleman et al. 2008, Connell et al. 2008,  
100 Mangialajo et al. 2008). Kelps provide substrata, food and shelter for a variety of  
101 organisms in different trophic levels and are important primary producers (Schiel and  
102 Foster 2006). Their high rates of productivity, e.g.  $1 - 2 \text{ kg C m}^{-2} \cdot \text{year}^{-1}$  (Mann 1982,  
103 Smale et al. 2013) are comparable to some of the most productive terrestrial systems,  
104 e.g. tropical rain forests produce up to  $1.7 \text{ kg C m}^{-2} \text{ year}^{-1}$  (Schuur 2003). Moreover,  
105 kelp detritus is an important vector of trophic connectivity, subsidising several coastal  
106 habitats such as beaches, rocky shores and seagrass beds (Krumhansl and Scheibling  
107 2011, 2012).

108 Changes in the abiotic environment (Suh et al. 2004, Suh et al. 2014) together  
109 with altered trophic relationships in urban estuaries (Faeth et al. 2005, Jackson 2009,  
110 Fischer et al. 2012) can indirectly affect functional properties of kelps. Examples  
111 include changes in light availability and water flow (e.g. Marzinelli et al. 2009,  
112 Marzinelli et al. 2011), potentially influencing their growth and/or erosion rates and  
113 the promotion of fouling on kelp blades (Marzinelli 2012), which can affect their  
114 photosynthetic capacity. Regardless of changes in their overall abundance, impacts on  
115 the growth and photosynthetic capacity of seaweeds have direct implications for the  
116 overall primary productivity of the habitats they form. Focus is usually given to  
117 assessments of their total abundance or presence/absence at particular place(s) at any  
118 given time, even though sub-lethal impacts on key species may have important  
119 implications for ecosystem functioning, (Harding et al. 2001). Therefore, impacts on  
120 functional physiological performances of habitat-forming species are potentially a

121 severely underestimated mechanism of environmental impact on ecosystem  
122 functioning.

123         This study was done in Sydney Harbour, an estuary with the greatest  
124 urbanised catchment in Australia, and residence of one-fifth of the countries'  
125 population (Johnston et al. 2015). Sydney Harbour can be broadly divided into 2  
126 locations: an inner and an outer zone, based on physical conditions and contamination  
127 and urbanisation levels. The inner area of the Harbour (hereafter referred to as Inner  
128 Harbour) is heavily urbanised and has a legacy of industrialisation and high  
129 contamination levels. In contrast, the outer zone (hereafter Outer Harbour) has greater  
130 oceanic flushing and wave exposure, sandier sediments and is moderately urbanized  
131 with lower levels of contamination (Dafforn et al. 2012b, Clark et al. 2015, Johnston  
132 et al. 2015, Mayer-Pinto et al. 2015). Many of these anthropogenic and natural  
133 stressors are spatially correlated, so their individual effects cannot be distinguished  
134 without manipulative experiments. Nevertheless, they represent different levels of the  
135 ecological footprint of human activities on the Harbour (Clark et al. 2015).

136         The main habitat-forming kelp found in Sydney Harbour is *Ecklonia radiata*  
137 (Johnston et al. 2015), a dominant foundation species present along 8,000 km of  
138 temperate coastal Australia (Marzinelli et al. 2015b). Kelps underpin great diversity  
139 and services estimated as worth > AU\$500 million year<sup>-1</sup> (Bennett et al. 2016). This  
140 study aimed to compare growth and erosion rates (i.e. how the blades of individual  
141 kelps eroded through time) of *E. radiata*, as well as its photosynthetic efficiency and  
142 total length, between natural and artificial habitats in areas with different levels of  
143 environmental stressors (i.e. Inner and Outer Harbour). We hypothesised that  
144 photosynthetic capacity and erosion rates of kelps would be less on pilings compared  
145 to natural reefs due to the low light availability, scouring and possible changes in

146 water flow. We also hypothesised that impacts of artificial structures on functional  
147 attributes of kelps would be more severe in the Inner Harbour, characterised by higher  
148 levels of human impacts and low flushing.

149

## 150 **Methods**

### 151 *Study Sites*

152 The study was done at four sites in Sydney Harbour in June 2014 (Figure 1).  
153 Two sites were selected from the inner harbour and were characterised by low oceanic  
154 input, high retention times, contamination and urbanisation. Two sites were selected  
155 from the outer harbour in areas of lower urbanisation, higher oceanic input and  
156 flushing (Dafforn et al. 2012b, Johnston et al. 2015, Mayer-Pinto et al. 2015). In  
157 winter, water temperature in the Harbour is often similar between zones, ranging  
158 between 16 and 20 °C in June, with salinity at these sites ranging from 35.2 to 35.6  
159 (Dafforn et al. 2012b, Johnston et al. 2015).

160 Pilings and rocky reefs were sampled at each site in the subtidal zone (~ 0.5 –  
161 2.0 m below MLWS). Pilings were vertical, with approximately 1 m diameter and  
162 made of wood. Pilings at the sampled sites were mainly part of public swimming  
163 pools surrounded by shark nets and wharves built over soft sediment (Figure 1).  
164 Natural reefs were of sandstone and mainly horizontal, with a gentle slope (Johnston  
165 et al. 2015). At each site, pilings and reefs were approximately 20 – 100 m apart. All  
166 sites had a minimum of 15 pilings present and only unshaded surfaces of pilings in the  
167 outer areas of wharves or swimming nets were sampled. This was done because those  
168 are often less shaded and harbour habitat-forming macro-algae.

169

### 170 *Macro-algae and invertebrate herbivores*

171 We determined the composition and density of habitat-forming seaweeds and  
172 ‘large’ invertebrate herbivores at artificial and natural habitats *in situ*. Sampling was  
173 done on the area of reefs and pilings that were occupied by habitat-forming macro-  
174 algae (~ 0.5 – 2.0 m deep) (Marzinelli et al. 2009, Marzinelli 2012). At each site, five  
175 quadrats of 50 x 50 cm were sampled and the number of invertebrates and large  
176 brown canopy-forming seaweeds counted. Many rocky shores in Sydney Harbour are  
177 fragmented and, therefore, shorter in extension than in areas with un-fragmented  
178 landscapes (Goodsell et al. 2007). This is particularly true at the Inner Harbour, where  
179 subtidal reefs are often much smaller than those found in Outer Harbour (Johnston et  
180 al. 2015). Natural reefs sampled here were not an exception and ranged from  
181 approximately 50 m long (in the Inner harbour) to 200 m (Outer Harbour). Therefore,  
182 although the total area sampled in each habitat at each site was arguably low (1.25  
183 m<sup>2</sup>), we believe that the area covered was enough for a representative sampling of the  
184 local habitats assessed. While this sampling plan was spatially extensive, we  
185 acknowledge that this is a temporal snapshot rather than an investigation of seasonal  
186 dynamics in these populations.

187

188



189

190 Figure 1 – Map of the sampling sites within the inner and outer areas of Sydney  
 191 Harbour. Pilings and natural reefs were found at all sites ~ 20 - 50 m apart.

192

193 *Functional measurements of Ecklonia radiata*

194 Growth and erosion rates of the kelp *Ecklonia radiata* were measured in the  
 195 austral winter (June-July 2014), using the traditional hole-punch method (Kirkman  
 196 1984). To measure growth, ten individual kelps at each site and type of habitat were  
 197 marked with two holes into the central lamina. The first hole was located 5 cm from  
 198 the junction between the stipe and the lamina and the second hole was 5 cm from the  
 199 first one. After approximately one month, the distance from the first hole to the  
 200 junction between the stipe–lamina and the distance between the two holes were  
 201 measured *in situ* (see e.g. Krumhansl and Scheibling 2011, De Bettignies et al. 2013).  
 202 Erosion was measured by punching one hole on the tip of the central lamina and two

203 other holes, vertically aligned, 5 cm distance from each other, below the tip. After one  
204 month, the total length of the algal individuals and distances between holes in each  
205 individual were measured to calculate erosion. For example, if, after a month, the  
206 distance between the tip and the first hole was 2 cm, erosion was estimated as 3 cm  
207 (i.e. the initial distance of 5 cm minus 2 cm). If only one hole was visible, it was  
208 assumed that at least 5 cm of the kelp had been eroded and total erosion was  
209 calculated based on the distance of the tip and the first visible hole + 5 cm. If,  
210 however, both holes had been eroded after a month, a conservative estimate of 10 cm  
211 erosion was made. The photosynthetic efficiency of *Ecklonia radiata* was measured  
212 using a Diving PAM (Pulse Amplitude Modulated, WALZ, Germany). PAM  
213 measurements were taken from the secondary lamina of 5 algae. To do this, algae  
214 were collected and measurements were done ex-situ. At each site, the collection of  
215 algae in the different habitats was done within one hour of each other to ensure  
216 similar environmental conditions. Measurements at each site were done in different  
217 days, randomly distributed, to avoid any possible confounding effects. All PAM  
218 measurements were done between 10 am – 1 pm, in similar light and temperature  
219 conditions. Sampled areas were dark-adapted for 15 minutes before measurements.  
220 The measurements used in this study was quantum yield ( $F_v/F_m$ ), which measures the  
221 photochemical efficiency of the algae (Marzinelli et al. 2015a).

## 222 *Statistical analyses*

223 Univariate tests for differences in response variables according to Habitat and  
224 Locations were tested with generalized linear mixed models (GLMMs) using the *lme4*  
225 package (Bates et al. 2011) in R v.3.0.1. Location (i.e. Inner vs Outer Harbour) and  
226 Habitat (i.e. pilings vs rocky reefs) were fixed factors, and Sites was random, nested  
227 in Location. We assumed Poisson distributions for counts, but when there was

228 significant overdispersion we used negative binomial. Tests to determine differences  
229 in the growth and erosion rates of kelps were done using Gaussian distributions. P-  
230 values were obtained with Likelihood Ratio Test (LRT) (Zuur et al. 2009). Post-hoc  
231 tests were done using the package *multcomp* in R v.3.0.1.

232

## 233 **Results**

### 234 *Macro-algae and invertebrate herbivores*

235 There were significantly more habitat-forming seaweeds - characterised by *E.*  
236 *radiata* and *Sargassum* spp. (LTR Chisq = 27.28; df = 1;  $p < 0.001$ ) - on natural rocky  
237 shores than on pilings (Fig 2). This was true even though abundance of macro-algae  
238 varied greatly among sites, being more abundant on pilings at Chowder Bay than in  
239 the reefs at this site (Figure S1). The higher abundance of macro-algae on reefs was  
240 mainly driven by *Sargassum* spp. (Fig X), which comprised 65% and 49% of the total  
241 algae found in the Inner and Outer harbour, respectively. Total algae abundance did  
242 not differ between locations (i.e. Inner vs. Outer Harbour; LTR Chisq = 2.57; df = 1;  
243  $p > 0.05$ ).

244 Similar to the patterns found in seaweeds, there were significantly more  
245 invertebrate herbivores (LTR Chisq = 39.00; df = 1;  $p < 0.001$ ) on natural reefs than  
246 on pilings (Figure 2). The herbivores mainly comprised the sea-urchin  
247 *Centrostephanus rodgersii* and limpets. Herbivores were only found, however, on the  
248 outer reefs of the Harbour (i.e. Chowder and Watsons Bay; Fig. 2 and Fig. S1).

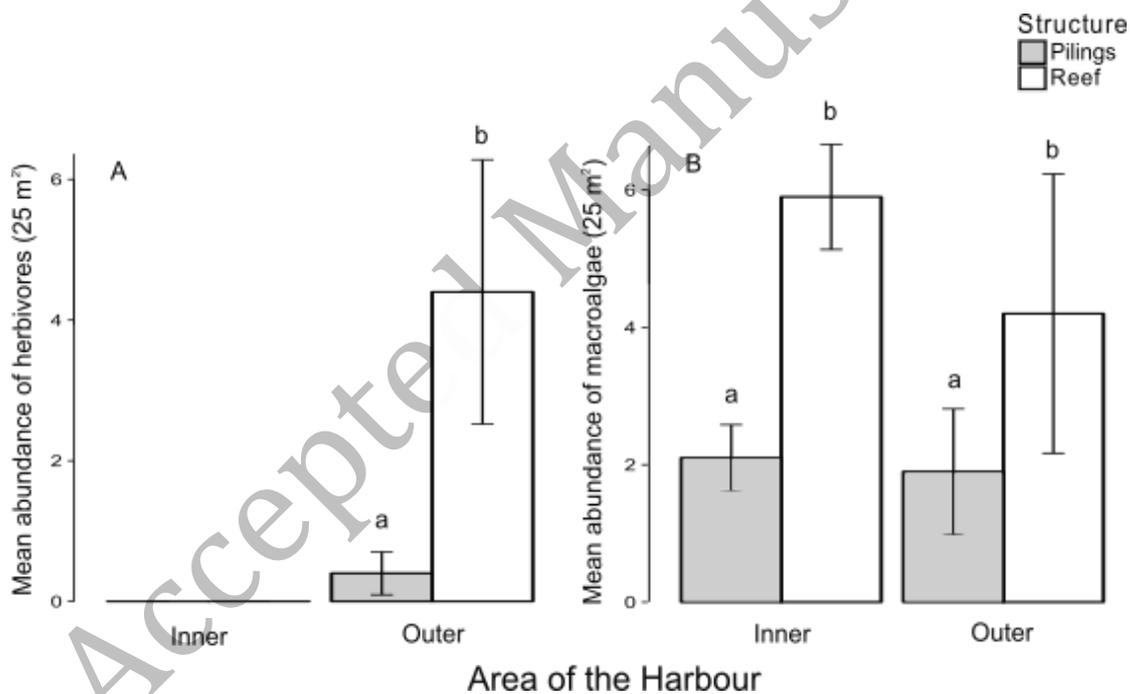
249

### 250 *Functional measurements of Ecklonia radiata*

251 Kelps on natural reefs had significantly greater erosion rates than kelps on  
252 pilings, regardless of the position in the estuary (inner or outer). There were, however,

253 no differences in the growth rates of *E. radiata* between types of habitat (Table 1; Fig  
 254 3), probably due to the great variability among sites, in particular at outer sites (Fig  
 255 S2). Although growth rates tended to be greater in the Outer Harbour, no statistical  
 256 differences were found between locations (Table 1; Fig. 3). In contrast, photosynthetic  
 257 activity of *E. radiata* was greater on kelps from outer compared to inner sites, but did  
 258 not differ between pilings and natural reefs. There were no significant differences in  
 259 the total length of kelps between habitats or locations (Table 1; Fig 3). Length of  
 260 kelps did varied greatly, however, among sites at the Outer Harbour, with contrasting  
 261 patterns between the two sampled sites at this zone (Fig S2).

262



263  
 264

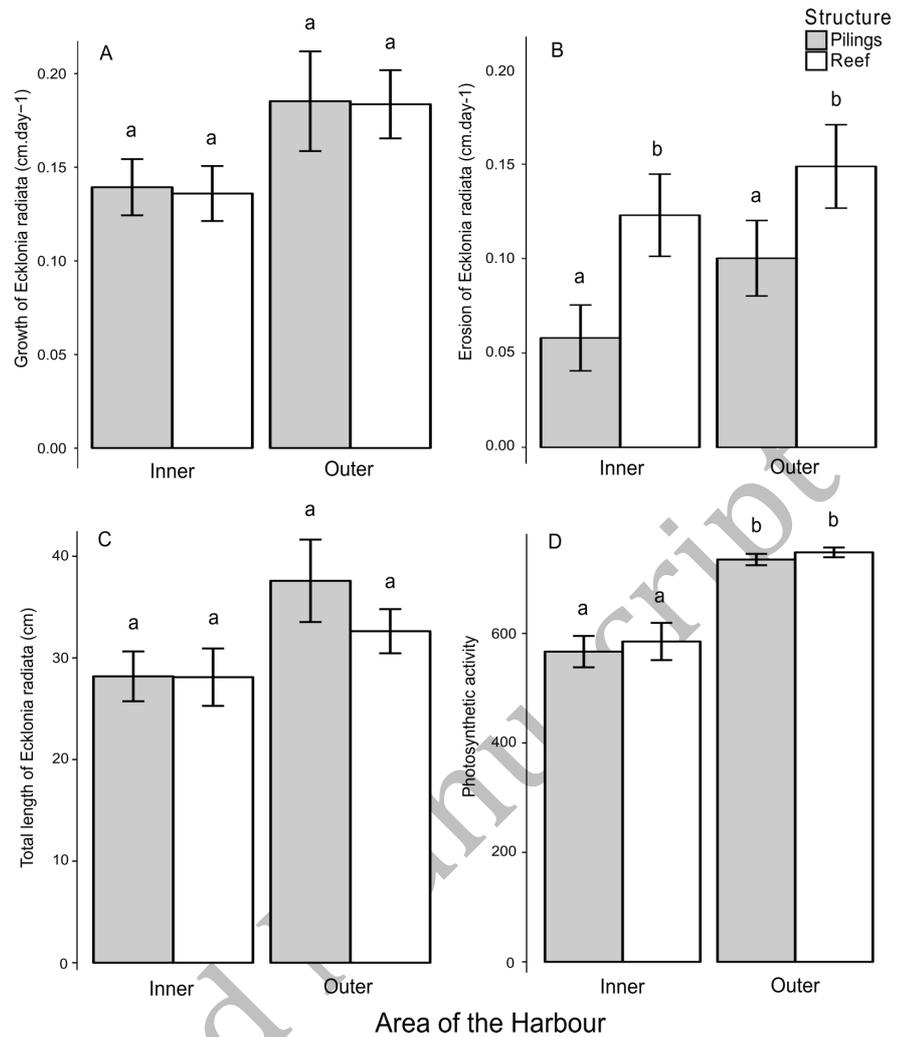
265 Figure 2 – Mean ( $\pm$  SE) abundance of herbivores (A) and macro-algae (B) found on  
 266 pilings (grey bars) or natural reefs (white bars) at locations situated in the Inner and  
 267 Outer part of Sydney Harbour. Only fixed factors are shown in the graphs as per  
 268 results from the statistical models. Different letters indicate where significant  
 269 differences lie.

270  
 271 Table 1. Analysis of deviance testing the effect of habitat (H; rocky shore and piling)  
 272 and location (L; Inner vs. Outer Harbour) on the photosynthetic efficiency, growth,  
 273 erosion rates and total length of the kelp *Ecklonia radiata* (Fig 3). Log-ratio chi  
 274 square statistic was used to assess significance.

275

	DF	Log ratio	P
<i>Photosynthetic efficiency</i>			
Habitat	1	0.53	0.467
Location	1	5.18	<b>0.023</b>
H X L	1	0.02	0.878
<i>Growth rates</i>			
Habitat	1	0.08	0.776
Location	1	2.93	0.087
H X L	1	0.01	0.904
<i>Erosion rates</i>			
Habitat	1	9.21	<b>&lt;0.01</b>
Location	1	3.10	0.078
H X L	1	0.49	0.485
<i>Total Length</i>			
Habitat	1	0.68	0.408
Location	1	2.05	0.153
H X L	1	0.73	0.394

276



277

278 Figure 3 - Mean (± SE) growth (A) and erosion rates (B) of the kelp *Ecklonia radiata*  
 279 as well as their total length (C) and photosynthetic activity (D) on pilings (grey bars)  
 280 and natural reefs (white bars) at locations situated in the Inner and Outer part of  
 281 Sydney Harbour. Only fixed factors are shown in the graphs as per results from the  
 282 statistical models. Different letters indicate where significant differences lie.

283

284 **Discussion**

285 This study is the first to reveal impacts on functional properties of key habitat-  
286 forming species from built infrastructure such as pilings in urban seascapes. Contrary  
287 to our predictions, effects of artificial structures on abundance and functioning of  
288 habitat-forming macro-algae were consistent across the different zones of the estuary,  
289 which was used here as a proxy for urban impact (e.g. physical modification and  
290 contamination). For example, macro-algae were more abundant on reefs than pilings  
291 in both inner and outer zones of the harbour. Moreover, kelps eroded more quickly on  
292 reefs than pilings regardless of location. Although we did observe decreases in  
293 photosynthetic activity at inner (and more impacted) sites, this was not related to  
294 habitat type (i.e. pilings vs. natural reefs). Given the importance of habitat-forming  
295 species, these results highlight the potential for artificial structures, and urban  
296 stressors or environmental variables, to affect the overall functioning of coastal  
297 habitats by impacting key functional properties of habitat-forming macro-algae. It is  
298 important to acknowledge that results here are from one-time point. Therefore, the  
299 magnitude and/or significance of differences found may change through time and/or  
300 with season.

301 The transfer and flow of energy (organic carbon) among habitats and  
302 ecosystems plays a critical role in shaping ecological process, influencing ecological  
303 dynamics from species interactions and food-webs to nutrient cycling and  
304 productivity of systems (Moore et al. 2004, Krumhansl and Scheibling 2012). In some  
305 systems (e.g. kelp forests), most of the energy created by primary producers is not  
306 consumed by herbivores, but returned to the environment as detritus, which is crucial  
307 for sustaining ecosystems (Moore et al. 2004, Krumhansl and Scheibling 2011). We  
308 found that habitat-forming macro-algae were at least two times more abundant on

309 natural reefs than on pilings regardless of the position in the estuary. This was mainly  
310 driven by *Sargassum* spp. Abundances of the kelp *Ecklonia radiata* did not differ  
311 between habitats, which confirms previous results by Marzinelli (2012). Nevertheless,  
312 this species eroded faster on natural reefs than on pilings regardless of the position in  
313 the estuary. These results suggest that, in places where artificial structures have  
314 replaced natural rocky habitats (e.g. some areas of Europe, such as Italy; Airoidi et al.  
315 2009) there is a likely decrease in the 'production' of macro-algal detritus. Kelps are  
316 believed to export over 80% of their primary production as detritus (Krumhansl and  
317 Scheibling 2012). This export has great consequences for the connectivity among  
318 habitats (Krumhansl and Scheibling 2012) and secondary productivity in adjacent and  
319 remote habitats (Filbee-Dexter and Scheibling 2014). Furthermore, kelps are now  
320 believed to play a substantial role as climate change regulators by acting as carbon  
321 donors to sites where detrital matters accumulate (Hill et al. 2015, Krause-Jensen and  
322 Duarte 2016). Kelp detritus may reach depositional areas, e.g. sediments or deep-sea,  
323 where the carbon is impeded from exchanging with the atmosphere (Krause-Jensen  
324 and Duarte 2016). *Sargassum* spp. is also believed to significantly contribute to  
325 detrital pathways in coastal systems (Wai et al. 2008). These algae displays seasonal  
326 changes in biomass, peaking in winter (Poore and Steinberg 1999) and dye or lose  
327 biomass when water temperatures increase (Kaehler and Williams 1996, Poore and  
328 Steinberg 1999). This results in large quantities of detached and decomposing macro-  
329 algae being exported to other habitats (Wai et al. 2008). The differences in abundance  
330 and erosion rates of key macro-algae described here can therefore have important  
331 implications for urbanised coastal environments across the globe.

332 Differences found here may change, however, through time. *Sargassum*, for  
333 instance, is an annual alga, with seasonal changes in biomass (Poore and Steinberg

334 1999). Therefore, when water temperatures are warmer, differences in abundances of  
335 macro-algae between natural and artificial habitats might not be present due to the  
336 general low abundances of *Sargassum*. In addition, population dynamics of *E. radiata*  
337 are known to vary through time and season (e.g. Kirkman 1984, De Bettignies et al.  
338 2013). Hence, differences found here might change in magnitude and/or significance  
339 according to season, year, etc. Further investigations that include temporal sampling,  
340 and done, ideally, at larger spatial scales, are necessary for us to have a clearer and  
341 broader picture of the impacts of artificial structures on key habitat-forming macro-  
342 algae and their full implications to the diversity and functioning of coastal systems.

343 Differences in the abundance of *Sargassum* spp. between habitats may be  
344 related to the type, orientation or position of substrata (Anderson and Underwood  
345 1994, Glasby and Connell 2001). While natural rocky shores in Sydney Harbour are  
346 mainly horizontal and composed of sandstone, pilings are vertical and often smoother  
347 and can be made of several types of material, such as wood and concrete (Glasby  
348 1999, Mayer-Pinto et al. 2015). Although spores of many macroalgae species show  
349 preference for colonising roughened surface (Watanuki and Yamamoto 1990, Fletcher  
350 and Callow 1992), this is unlikely to be the main factor driving the differences  
351 observed here. Watanuki and Yamamoto (1990)

352 . Grazing pressure can also affect the development of  
353 macroalgal assemblages (Kennelly 1983) and could have differed between pilings and  
354 reefs. Although we found more macro herbivores on natural reefs than on pilings, we  
355 did not assess meso-grazers (e.g. amphipods), which are known to graze on *Sargassum*  
356 (Poore and Steinberg 1999) and could therefore have influenced these results. Light  
357 levels might also have played a role in differential abundance between habitats,  
358 presumably by influencing the recruitment of sporophytes of *Sargassum* (Deysher and

359 Dean 1986), rather than the growth of adults given the lack of difference in  
360 photosynthetic ability of adult kelps on pilings and rocks. The reduced kelp erosion  
361 rates on pilings is likely due to the greater potential for scouring (abrasion) of kelp  
362 fronds on the reef (Kennelly 1989) compared to pilings and possible changes in water  
363 flow around these structures (Lagos et al. 2017). Further investigations are however  
364 needed to identify the mechanisms driving these patterns.

365 Macro-algal photosynthesis plays a critical role in the global primary  
366 production (Smith 1981). Surprisingly, photosynthetic efficiency of kelps was not  
367 affected by artificial structures, as hypothesised due to low light availability at these  
368 habitats. Instead, we found lower photosynthetic efficiency on kelps in the inner (and  
369 more impacted) areas of the Harbour (i.e. Inner Harbour). Kelp growth rates were also  
370 slightly greater in the outer areas of Sydney harbour (although no statistical  
371 differences were observed). The high levels of contamination present in the Inner  
372 Harbour (Birch and Taylor 2004, Dafforn et al. 2012b) could be driving these effects,  
373 adding to the usual impacts associated with the addition of artificial habitats. Equally,  
374 differences in turbidity between the inner and outer estuary (Clark et al. 2015), as well  
375 as possible differences in salinity that might occur seasonally (Johnston et al. 2015),  
376 could be driving differences in kelp growth and photosynthesis. These variables also  
377 influence the availability of heavy metals (e.g. Hatje et al. 2003). These added effects  
378 are expected to cause changes in the overall primary productivity of highly urbanised  
379 habitats dominated by these habitat-formers.

380 Management strategies such as eco-engineering of artificial structures can  
381 mitigate many of the impacts caused by the introduction of these artificial habitats in  
382 coastal systems (Dafforn et al. 2015). Examples include changes in the material and  
383 design of infrastructure, which could lead to reduced changes to water flow and

384 epibenthic and fish assemblages (Strain et al. in press), which could in turn affect  
385 kelps. These strategies need to be tailored, however, for the type of habitat and/or  
386 species being affected as well as the functions/services that can be potentially offset  
387 by these strategies. Pilings – the artificial structure studied here – are particularly  
388 pervasive in estuarine and coastal areas across the globe because they support boating  
389 related activities. These structures are therefore usually associated with the  
390 construction of marinas, where they are built for mooring boats (Glasby 1999) or  
391 private and/or public docks or wharfs. In Southeast Florida, US, alone, in the  
392 Loxahatchee River and estuary, Layman et al. (2014) counted a total of 13,554 dock  
393 pilings, each supporting a diverse fouling assemblage. Such structures are usually  
394 built in sedimentary habitats; considered one of the most impacted habitats by ocean  
395 sprawl (Davis et al. 1982, Martin et al. 2005, Heery et al. 2017). Consequently,  
396 strategies to offset impacts caused by these structures, such as those shown here,  
397 should include not only ways to minimise impacts on kelps, but also to offset the loss  
398 of soft sediment communities and the services they provide (see e.g. Heery et al.  
399 2017).

400

#### 401 **Conclusion**

402 We showed that the compounding effects of human development on coastlines  
403 worldwide have the potential to significantly influence the functioning of coastal  
404 habitats, in particular estuaries, through effects on functional properties of key  
405 species, such as the kelp *Ecklonia radiata*. Integrated management strategies to  
406 mitigate impacts on foundation species by, not only coastal development, but also by  
407 other anthropogenic activities (e.g. industrialisation) are necessary to ensure the  
408 continuing provision of services of these important systems.

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414

415 **Authors' contributions**

416 MMP, KAD, TMG and ELJ conceived the ideas and designed the surveys. MMP,  
417 KAD, and AB collected the data. MMP analysed the data and led the writing of the  
418 manuscript. All authors contributed critically to the drafts and gave final approval for  
419 publications.

420

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